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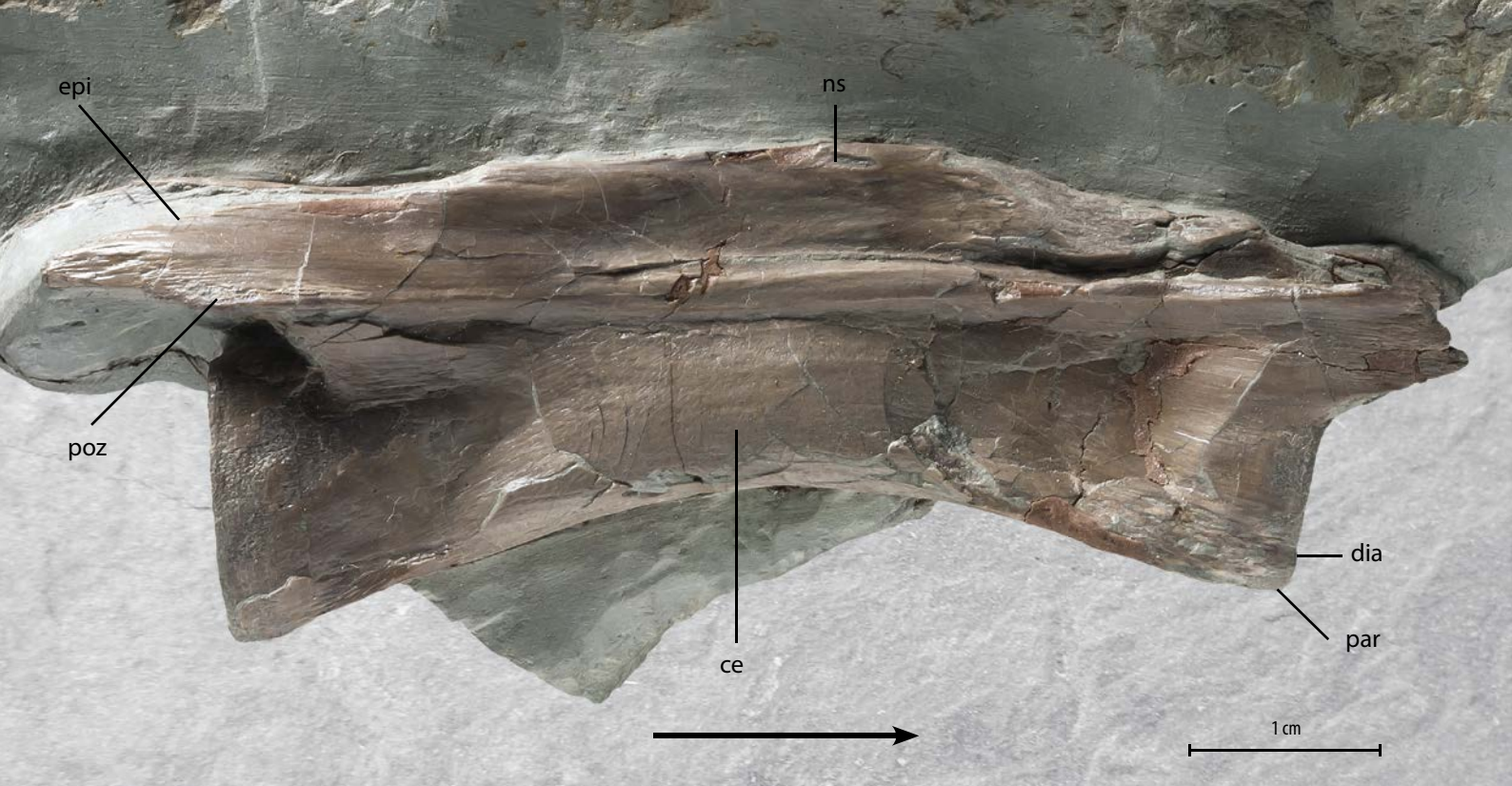


FIGURE 1. | Isolated mid-cervical Coll. Oosterink A638 in right lateral view, the original specimen described by Wild & Oosterink (1984). The arrow points anteriorly. Abbreviations: ce, vertebral centrum; dia, diapophysis; epi, epipophysis; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis. Photograph courtesy of Nicole Klein.

Tanystropheids from the Winterswijk quarry - rare but recurring elements

U vindt een samenvatting aan het eind van de tekst.

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Abstract | Tanystropheids were archosauromorph reptiles from the Triassic characterized by long necks composed of elongate cervical vertebrae and ribs, as is epitomized by its most recognisable genus *Tanystropheus*. An isolated cervical vertebra from the Winterswijk quarry was assigned to *Tanystropheus antiquus* in 1984. However, the genus *Tanystropheus* has been repeatedly revised and the taxonomic status of *Tanystropheus antiquus* has been questioned since. Furthermore, the taxonomic affinity of the growing body of tanystropheid material from Winterswijk has not formally been investigated, rendering the identity of tanystropheid material from the Vossenveld Formation uncertain. We present an overview of the taxonomic history of *Tanystropheus* in order to clarify the identification of tanystropheid remains from the Lower Muschelkalk, including those from Winterswijk. Furthermore, we present and describe several previously unpublished tanystropheid specimens from the Winterswijk quarry. Although conclusive taxonomic assignment of exclusively isolated elements is problematic, all presented cervical vertebrae are tentatively assigned to ‘*Tanystropheus antiquus*’. The other unequivocally tanystropheid remains, two cervical ribs and a dorsal vertebra, are identified as *Tanystropheus* sp.

A brief overview of Tanystropheidae

Tanystropheidae were a group of Triassic archosauromorphs, the lineage also including crocodylians, pterosaurs, and dinosaurs including birds, characterized by long necks made up of conspicuously elongated cervical vertebrae and ribs. This clade presently encompasses circa eight genera as well as a few additional but poorly known taxa. Its most iconic member is *Tanystropheus longobardicus*, an extremely long-necked reptile represented by a number of articulated specimens from the Monte San Giorgio strata of Switzerland and Italy (Wild, 1973; Nosotti 2007), with another specimen from China likely also belonging to this species (Rieppel *et al.*, 2010). *T. longobardicus* reached a total body length of up to six meters (following Wild, 1973) and featured a neck composed of 13 extremely elongated cervical vertebrae associated with even longer cervical ribs that collectively formed a light-weight and very stiff neck (Tschanz, 1986). Although dentition and stomach contents unequivocally indicate that the diet of the large specimens of *T. longobardicus* included fish and squid, current interpretations of its palaeobiology range from a semiaquatic lifestyle with largely terrestrial affinities to a fully aquatic lifestyle (e.g. Wild, 1973; Tschanz, 1988; Renesto, 2005; Nosotti, 2007). Tanystropheidae furthermore included obligate terrestrial genera, such as *Macrocnemus* (Peyer, 1937; Jaquier *et al.*, 2017) and

Langobardisaurus (Renesto, 1994; Renesto & Dalla Vecchia, 2000), and aquatic taxa, such as *Tanytrachelos* (Olsen, 1979) and *Dinocephalosaurus* (Li *et al.*, 2004; Rieppel *et al.*, 2008). The latter genus exemplifies a particularly striking demonstration of tanystropheid evolutionary plasticity, since *Dinocephalosaurus* attained a similar body size as *Tanystropheus* and featured a correspondingly long neck. However, whereas the long neck of *Tanystropheus* consisted of only 13 extremely elongated cervical vertebrae (Rieppel *et al.*, 2010), the neck of *Dinocephalosaurus* comprises at least 27 comparatively shorter cervicals (Rieppel *et al.*, 2008). Furthermore, an exclusively marine lifestyle for *Dinocephalosaurus* is well established through its flipper-like appendages (as indicated by hyperphalangy) and evidence for viviparity (i.e. giving birth to live young rather than laying eggs) (Liu *et al.*, 2017). These observations indicate that these structures may have had different functional properties and that the acquisition of an extremely elongated neck is homoplastic for these two taxa, meaning that extreme neck elongation occurred at least twice in the course of tanystropheid evolution. Their morphological diversity, biogeographical distribution, and occurrence in a myriad of different environments render Tanystropheidae a remarkably diverse group of Triassic archosauromorphs.

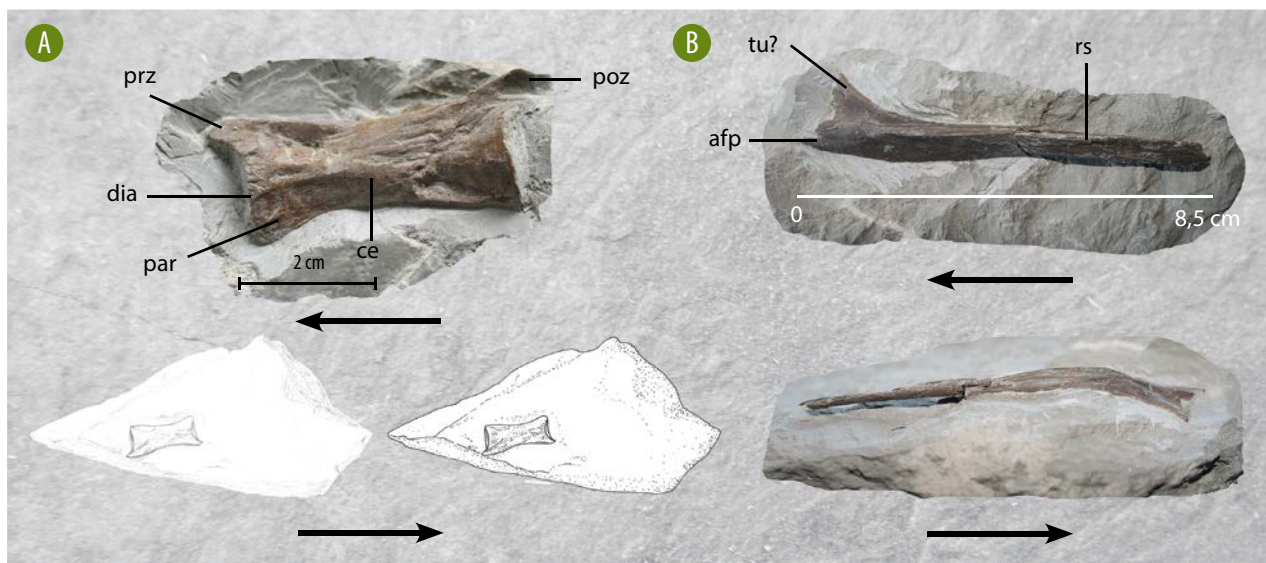


FIGURE 2. | Material from the collection of Adriaan and Marc Dorst assigned to *Tanystropheus*. (A) A cervical vertebra assigned to ‘*T. antiquus*’ shown in lateroventral view. Top, photograph; bottom, interpretative drawings. (B) A likely posterior cervical rib assigned to *Tanystropheus* sp. Top photograph in lateral or medial view; bottom photograph in dorsal view. The arrows point anteriorly. Abbreviations: afp, anterior free-ending process; ce, vertebral centrum; dia, diapophysis; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis; rs, rib shaft; tu, tuberculum. Photographs and interpretative drawings by Adriaan and Marc Dorst.



From a systematic perspective, Tanystropheidae were considered to fall within the larger clade of ‘Proto-roosauria’ or ‘Prolacertiformes’; groups named after *Protorosaurus speneri* (Gottmann-Quesada & Sander, 2009) and *Prolacerta broomi* (Gow, 1975; Modesto & Sues, 2004; Spiekman, 2018), respectively. However, recent phylogenetic analyses demonstrated the polyphyly of these groups (Pritchard *et al.*, 2015; Ezcurra, 2016). Tanystropheids therefore currently form their own designated monophyletic clade within early Archosauromorpha.

Tanystropheus in the Lower Muschelkalk

The only tanystropheid material from the Vossenveld Formation (Lower Muschelkalk, Anisian, Middle Triassic) that has thus far been described in detail constitutes an isolated cervical vertebra (Wild & Oosterink, 1984; Coll. Oosterink A638; Fig. 1). The specimen was interpreted to originate from the central to posterior part of the cervical column and assigned to *Tanystropheus antiquus* (see also Oosterink *et al.*, 2003). The current taxonomic status of *T. antiquus* is equivocal, which has created confusion regarding the taxonomic identity of the referred vertebra and other tanystropheid elements from the Vossenveld Formation. Representative material from Winterswijk is currently collectively attributed to *Amotosaurus rotfeldensis* (e.g. Sander *et al.*, 2014; Heijne *et al.*, 2019). In order to properly evaluate the tanystropheid material from Winterswijk, most of which is housed in private collections, an overview of the taxonomic history of *T. antiquus* will first be provided.

Between the 1920s and 1980s, a number of articulated specimens, including several nearly complete skeletons, were discovered and described from the Grenzbitumenzone (Anisian-Ladinian boundary; Stockar, 2010) of the Monte San Giorgio mountain on the border between Switzerland and Italy (Peyer, 1931; Wild, 1973; Wild, 1980a). This material shared particular similarities with a specimen previously found on the same mountain, which was at the time identified as a pterosaur, *Tribelesodon longobardicus* (Bassani, 1886; Nopsca, 1923). The most convincing agreements were the tricuspid form of the marginal dentition and the

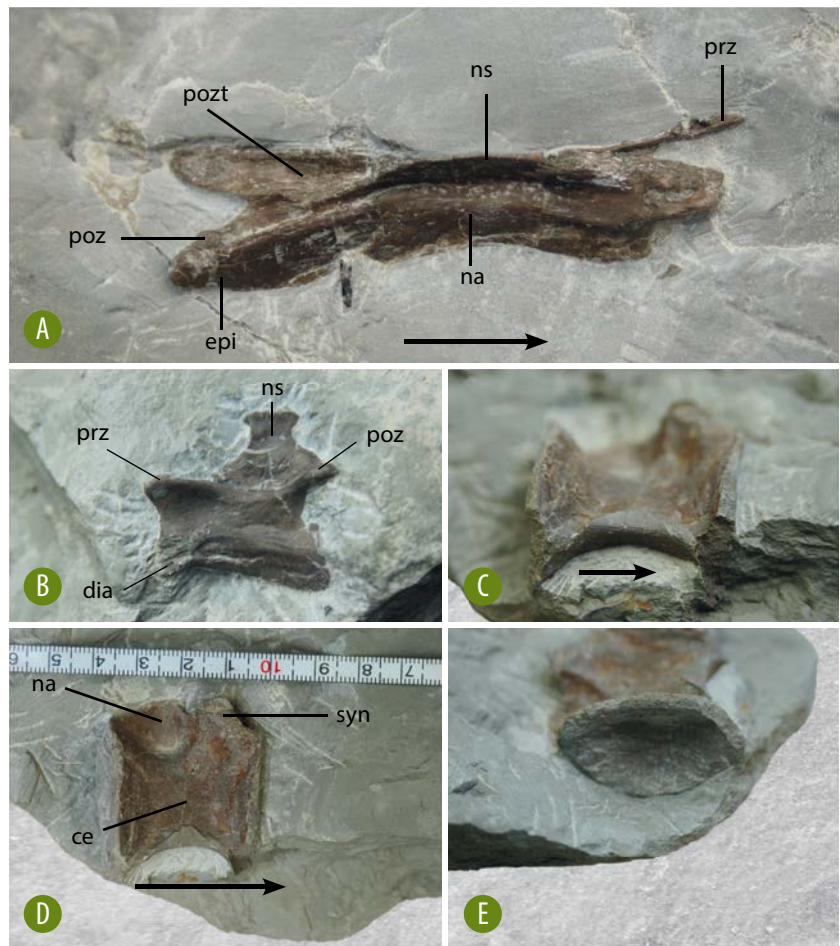


FIGURE 3. | Material from the collection of Remco Bleeker assigned to *Tanystropheus*. (A) A cervical vertebra assigned to '*T. antiquus*' in angled dorsal view. (B) A posterior cervical vertebra assigned to '*T. antiquus*' in left lateral view. (C/D/E) A dorsal vertebra assigned to *Tanystropheus* sp. in angled ventral view (C), ventrolateral view (D) and angled posterior view (E). The arrows point anteriorly. Abbreviations: ce, vertebral centrum; dia, diapophysis; epi, epiphysis; na, neural arch; ns, neural spine; poz, postzygapophysis; poz, postzygapophyseal trough; prz, prezygapophysis; syn, synapophysis. Photographs by Remco Bleeker and Nicole Klein.

elongated cervical vertebrae that, in the pterosaurian interpretation, had been held for elongated phalanges that supported the wing membrane. However, similarly elongated vertebrae had earlier been recovered from the Upper Muschelkalk (late Anisian to early Ladinian) of Germany and subsequently described as *Tanystropheus conspicuus* (Meyer, 1855). Because the new finds from the Monte San Giorgio clearly demonstrated that the characteristic cervical vertebrae were very similar to the *T. conspicuus* vertebrae, the Monte San Giorgio taxon was renamed *Tanystropheus longobardicus* (Peyer, 1931). At the same time, more complete insight into the morphology of *Tanystropheus* allowed for the recognition of many isolated remains from the Muschelkalk as elements also belonging to the genus *Tanystropheus* (Huene, 1931). The isolated nature of these remains had seen them previously assigned to different taxa of varying affinities (see pag. 148-151 in Wild, 1973 for a synonymy list). The *Tanystropheus* material from the Upper Muschelkalk (and the slightly younger Lettenkeuper (Ladinian); Mennig & Hendrich, 2016), which exhibited the greatest similarities with *T. longobardicus*, was assigned to *T. conspicuus*. The material from the Lower Muschelkalk differed more evidently from *T. longobardicus* in having distinctly shorter cervical vertebrae with more pronounced neural spines and zygapophyses (Wild, 1973), and was therefore assigned to *T. antiquus*. That name was first given to several elongate vertebrae from the Lower Muschelkalk of the well-known Gogolin beds near Gogolin and Krapkowice in Silesia, Poland (Huene, 1907-1908).



More tanystropheid material was described from the Upper Buntsandstein (early Anisian) of the German Black Forest, which is slightly older than Lower Muschelkalk deposits. This material was assigned to *T. longobardicus* and *Macrocnemus bassanii* (Ortlam, 1966). Wild revised this material and reassigned it to *T. antiquus* (Wild, 1980b). Later, newly prepared material from the Buntsandstein locality led Wild to suppose that *T. antiquus* actually represented a distinct genus closely related to *Tanystropheus* and *Macrocnemus*. However, he refrained from substantiating this new genus at that time (Wild, 1987). Fraser & Rieppel (2006) provided a reassessment of the *T. antiquus* material and followed up on the preliminary assessment by Wild. They found that the material from the Buntsandstein, which encompasses multiple articulated specimens, indeed disagreed with the generic diagnosis for *Tanystropheus* and assigned it to the new taxon *Amotosaurus rotfeldensis*. The main differences with *T. longobardicus* are the number of cervical vertebrae, eight for *Amotosaurus* and 13 for *T. longobardicus* (previously considered to be 12, see Rieppel *et al.*, 2010), and the body size, since Fraser & Rieppel showed that the much smaller *Amotosaurus* specimens likely represented adult individuals because of their well-ossified tarsus. Additional but smaller morphological differences are provided in the diagnosis of *Amotosaurus rotfeldensis* (Fraser & Rieppel, 2006).

Fraser & Rieppel (2006) also evaluated the status of *T. antiquus* from the Lower Muschelkalk, including the isolated cervical vertebra from the Vossenveld Formation described by Wild & Oosterink (1984), and discussed deviations from *T. conspicuus* and *T. longobardicus*. First of these is the different spatial and temporal (i.e. earlier) distribution, which they acknowledged does not offer valid grounds for specific identification. Since only a small number of isolated cervical vertebrae are presently available, opportunities for morphological comparison are limited. However, observable differences do include the relatively smaller size and the aberrant shape of the cervical vertebrae, which are comparatively shorter and carry taller neural spines. Furthermore, the shape of all known cervicals of *T. antiquus* corresponds with those of the most posterior cervical vertebrae of *T. conspicuus* and *T. longobardicus*. However, Fraser & Rieppel pointed out that the complete absence of more elongated mid-cervical vertebrae in Lower Muschelkalk deposits is extremely unlikely to represent a preservational or sampling bias, since numerous shorter cervical vertebrae attributed to *T. antiquus*

are known, yet more elongate elements are completely absent. This observation suggests that cervical vertebrae assigned to *T. antiquus* were indeed shorter than those of other *Tanystropheus* species, which prompted them to provisionally maintain the species *T. antiquus*. Nevertheless, in the absence of additional bones and more complete specimens that would allow for a definitive comparison, they also recognised that the available material of *T. antiquus* does formally not permit a sufficiently defined diagnosis. They used the relatively shorter length of the cervical vertebrae in their diagnosis to distinguish this species from other *Tanystropheus* species and it is important to note that therefore only cervical vertebrae can be referred to *T. antiquus* through this diagnosis.

Sennikov (2011) described a number of isolated bones, mostly comprising cervical vertebrae but also including a few dorsal vertebrae and partial femora, from the latest Olenekian (Early Triassic) of Russia. This material accounts for some of the earliest known tanystropheid elements (see also De Oliveira *et al.*, 2018) and was assigned to the new taxon *Augusta-buriania vatagini*, which is considered morphologically closest to *T. antiquus*

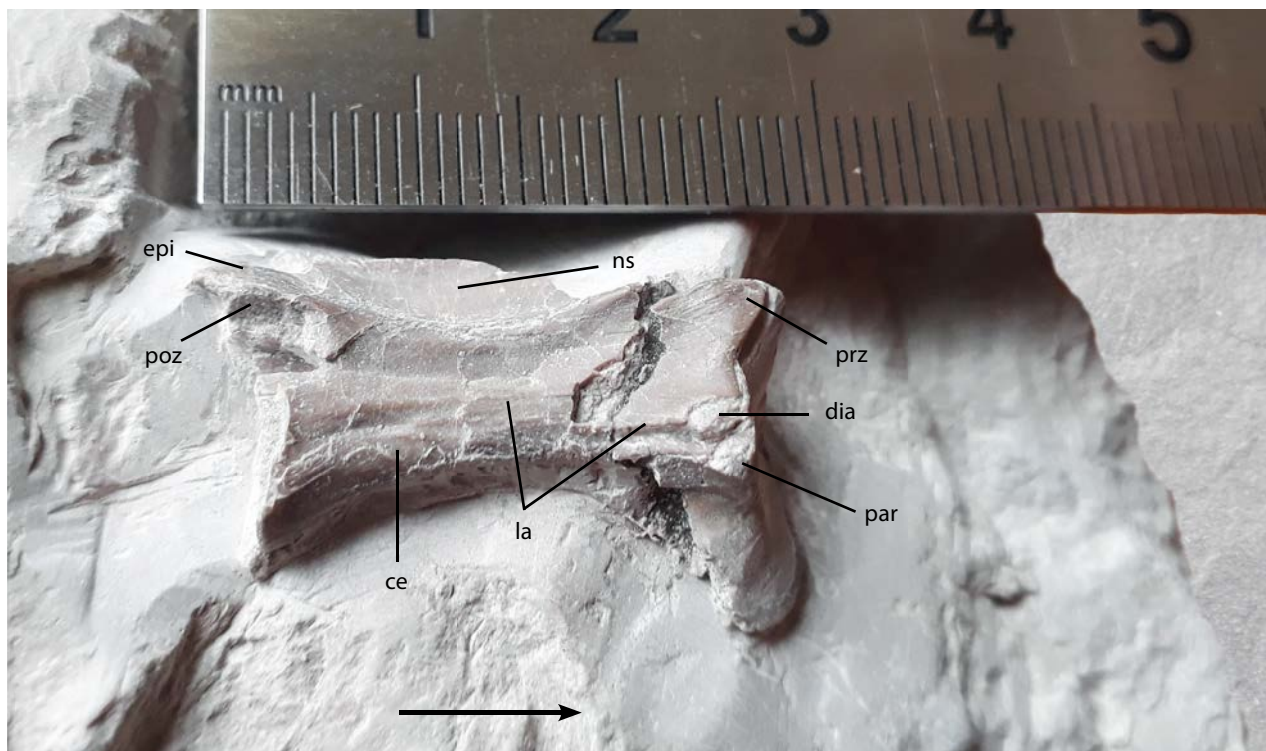


FIGURE 4. | A cervical vertebra from the collection of Richard de Haan referred to '*T. antiquus*' in angled right lateral view. The arrow points anteriorly. Abbreviations: ce, vertebral centrum; dia, diapophysis; epi, epipophysis; la, lamina; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis. Photograph by Richard de Haan.



and *Amotosaurus*. Unfortunately, as with *T. antiquus*, this material consists of few isolated remains, which prevents an accurate description and diagnosis. Furthermore, Sennikov did not provide a detailed comparison of *A. vatagini* with *T. antiquus* and *Amotosaurus*, but did reconsider the position of *T. antiquus* within the genus *Tanystropheus*. He concluded that *T. antiquus* differed generically from the other *Tanystropheus* species and therefore referred it to the new genus *Protanystropheus*.

Recently, in their revision of Triassic archosauromorph material from Poland, Skawiński *et al.*, (2017) studied the specimens from the Gogolin beds used in the original description of *T. antiquus* by Huene (1907–1908). They noted several flaws in the diagnosis of *Protanystropheus* and therefore restored *T. antiquus* to the genus *Tanystropheus* based on the material from Gogolin. They furthermore expressed that the confident assignment of tanystropheid material from other European localities, including Winterswijk, to *T. antiquus* would first require a more detailed revision of the original material from Gogolin, which is ongoing (pers. comm. Tomasz Szczygielski).

Although the status and distribution of *T. antiquus* is currently unclear, the presence of a long-necked tanystropheid with close affinities to *T. longobardicus*, *T. conspicuus*, *Amotosaurus*, and likely *Augustaburiania* in Lower Muschelkalk assemblages is evident. Besides the Vossenveld and Gogolin formations, isolated material previously identified as *T. antiquus* (but currently not considered to belong to this species sensu Skawiński *et al.*, 2017) has been reported from other Lower Muschelkalk deposits at Rüdersdorf near Berlin, Jena (northern to central eastern Germany), and possibly Bonnhof (southwestern Germany; Wild, 1980a, Wild, 1980b).

Tanystropheidae from the Vossenveld Formation

Since the description of the isolated cervical vertebra (Coll. Oosterink A638; Fig. 1) by Wild & Oosterink (1984), several additional isolated tanystropheid elements have been encountered in the Winterswijk quarry, which are presented here. These elements constitute a number of cervical vertebrae, a partial dorsal vertebra, a largely complete posterior cervical rib, and two partial shafts of anterior to mid-cervical ribs (Figs. 2–7). Although relatively rare, tanystropheid material is occurs throughout most of the Vossenveld stratigraphy exposed in the Winterswijk quarry. Recent excavation efforts predominantly focus on the interval surrounding Layer 9 (sensu Oosterink, 1986), which has produced most of the elements presented here.

Nevertheless, Coll. Oosterink A638 (Fig. 1) was recovered from an unknown horizon younger than Layer 12 (sensu Oosterink, 1986; Wild & Oosterink, 1984), and a diagnostic tanystropheid cervical was found in the strongly mineralized ('Galenite') Layer 29 (sensu Oosterink, 1986) as well (personal observation D.F.A.E.V.).

Since Skawiński *et al.* (2017) did not provide a formal revised diagnosis for *T. antiquus* from the Gogolin Formation, the diagnosis of Fraser & Rieppel (2006), which exclusively rests on cervical morphology, is followed here. Therefore it is only possible to refer cervical vertebrae to *T. antiquus* until a formal and more complete revision of the species is provided. The cervicals all

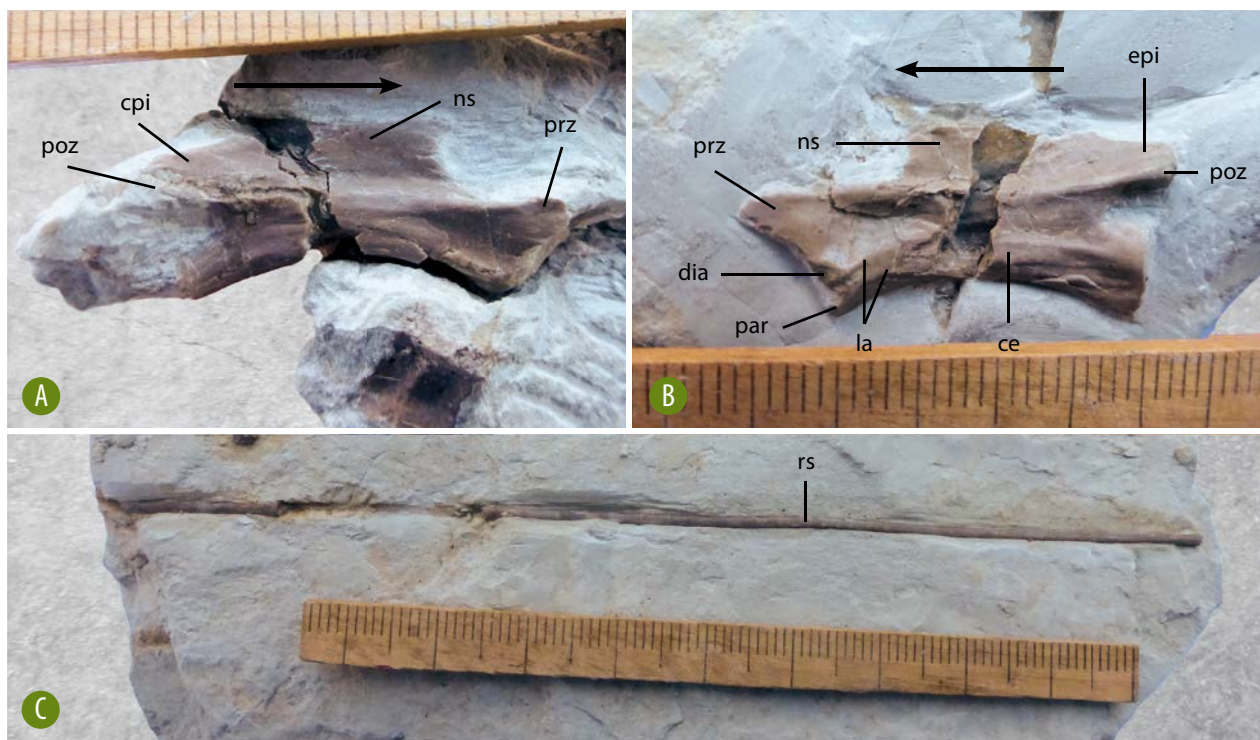


FIGURE 5. | Material from the collection of Herman Winkelhorst assigned to *Tanystropheus*. (A) Partial cervical vertebra in right lateral view assigned to '*T. antiquus*'. (B) Cervical vertebra in left lateral view assigned to '*T. antiquus*'. (C) Partial rib shaft of an anterior to middle cervical rib assigned to *Tanystropheus* sp. The arrows point anteriorly. Abbreviations: ce, vertebral centrum; dia, diapophysis; epi, epipophysis; la, lamina; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis; rs, rib shaft. Photographs by Herman Winkelhorst.



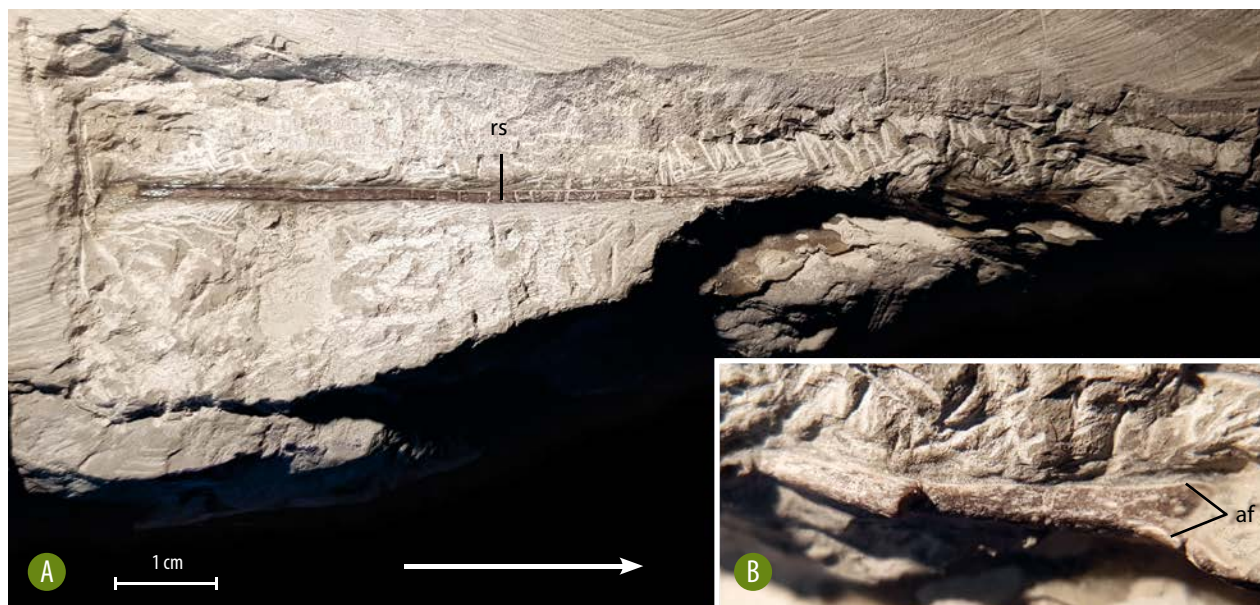


FIGURE 6. | A partial isolated cervical rib from the collection of Rolf Harmelink assigned to *Tanystropheus* sp. (A) The complete specimen. (B) Close up of the articular head of the rib exhibiting the two vertebral articulation facets in dorsal view. The arrow points anteriorly. Abbreviations: af, articular facet; rs, rib shaft. Photographs courtesy of Melanie During.

exhibit morphologies that agree with this diagnosis and are therefore assigned to '*T. antiquus*' (quotation marks are used in recognition of the uncertain taxonomic status of this species). The two isolated rib elements and the dorsal vertebra are indistinguishable from *T. conspicuus* and *T. longobardicus*, as well as from a dorsal vertebra assigned to '*T. antiquus*' by Huene (1931, Fig. 16, pag 78), and are therefore identified as *Tanystropheus* sp.

The isolated cervical vertebra described by Wild & Oosterink (1984) likely originated from the middle part of the neck based on the small size of its neural spine, which is reduced in the mid-cervicals relative to the anterior and posterior cervicals (Fig. 1). The ventral margin of the vertebral centrum is distinctly concave; a character shared by '*T. antiquus*' and *Amotosaurus*, but not agreeing with the more straight ventral margin of the cervical vertebrae of *T. longobardicus* and *T. conspicuus*.

The collection of Adriaan and Marc Dorst includes an unambiguous tanystropheid cervical vertebra (Fig. 2A) and an isolated element that is tentatively identified as a posterior cervical rib (Fig. 2B). The vertebra is exposed in ventrolateral view and clearly exhibits the articulation facets for a cervical rib (i.e. diapophysis and parapophysis; Fig. 2A). Although somewhat smaller and less elongate, its morphology strongly agrees with that of Coll. Oosterink A638. Because it is comparatively less elongate, it was likely located further posteriorly on the cervical column. The other element is identified as a posterior cervical rib based on similarities with corresponding elements in *T. longobardicus* (e.g. PIMUZ T 2817 and PIMUZ T 1277). As in all tanystropheids, the length of the cervical vertebrae is comparatively much shorter at the base of the neck (the posteriormost two or three vertebrae), and their corresponding ribs are also much shorter and stockier, yet they are still oriented parallel to vertebral column and are excluded from the thoracic rib cage.

Two cervical vertebrae and a dorsal vertebra are present in the collection of Remco Bleeker (Fig. 3). One cervical vertebra preserves the neural arch, including both zygapophyses, and a low neural spine, indicating that it likely represents a mid-cervical vertebra (Fig. 3A). The vertebral centrum remains encased in matrix but the specimen clearly exhibits the postzygapophyseal trough as described for *Tanystropheus haasi* from the Muschelkalk of Israel. This trough is flanked laterally by the vertically oriented medial margin of the epipophysis that resides on top of the postzygapophysis. The other cervical

vertebra (Fig. 3B) is visible in left lateral view and is complete. It is identified as a posterior cervical vertebra based on its comparatively short length, which is typical of the posterior cervical vertebrae in tanystropheids. It differs from dorsal vertebrae in having a dia- and parapophysis located closely together on the anteroventral portion of the centrum. The parapophysis is not visible in left lateral view as it is covered by the laterally extending diapophysis. The neural spine has a flat dorsal margin and is somewhat anteroposteriorly expanded on its dorsal end. The dorsal vertebra (Fig. 3C-E) is exposed in right lateroventral view and lacks most of the neural arch, including the neural spine and both zygapophyses. The vertebra appears indistinguishable from the poorly known dorsals of '*T. antiquus*' as described by Huene (1931, Fig. 16, pag 78), but a more detailed comparison is possible with the dorsal vertebrae of *T. conspicuus* and *T. longobardicus*. The vertebra shares the following characters with these taxa: amphicoelous articular surfaces of the centrum, the very narrow width of the ventral portion of the centrum, and the lack of a ventral keel (Fig. 3C-E). These shared characters identify the specimen as *Tanystropheus* sp. The vertebra is furthermore characterized by the presence of a synapophysis (i.e. a single articulation for the dorsal rib



resulting from a confluence of the dia- and parapophysis), which also occurs in the middle to posterior dorsal vertebrae of *T. longobardicus* and *T. conspicuus*. Because more anterior dorsals bear a separate dia- and parapophysis, this specimen is considered a mid to posterior dorsal vertebra.

Another isolated cervical vertebra is housed in the collection of Richard de Haan. This small specimen likely represents a mid-cervical vertebra because of its low neural spine and relative elongation (Fig. 4). It is visible in right lateral view and its exceptional preservation allows for the observation of several traits in detail. These include the slight posterior overhang of the neural spine, the presence of the epipophysis dorsal to the postzygapophysis, the location of the dia- and parapophysis with which the corresponding rib would have articulated, and the presence of two horizontal laminae on the lateral surface of the vertebral centrum. The more dorsally located lamina runs along the entire anteroposterior length of the centrum, whereas the more ventrally located lamina originates at the diapophysis and runs posteriorly for approximately half the length of the centrum.

The collection of Herman Winkelhorst includes two cervical vertebrae and a partial cervical rib (Fig. 5).

Both vertebrae share overall shape and size with the cervical vertebra in the collection of Richard de Haan (Fig. 4). In the more complete of the two specimens (Fig. 5B), the dia- and parapophysis are well preserved, as are aspects of the two laminae. Both vertebrae originate from the mid-cervical region. The incomplete cervical rib is round in cross section and extremely thin and straight, which is a diagnostic feature of the mid-cervical ribs of tanystropheids. Because they are considerably longer than their respective vertebrae, these ribs would have overlapped during life, thereby forming a rigid bundle ventral to the vertebrae in support of the long and stiff neck (Tschanz, 1986; Jaquier & Scheyer, 2017). Nevertheless, the rib measures 131 mm in preserved length and therefore exceeds the size of the vertebrae distinctly and must have originated from a much larger individual. Due to the lack of diagnostic characters, this specimen is tentatively assigned to *Tanystropheus* sp.

Another partial cervical rib is present in the collection of Rolf Harmelink (Fig. 6). It is similar to the rib in the collection of Herman Winkelhorst but additionally preserves the articulation facets with the vertebra anteriorly (Fig. 6B). Because the rib is isolated, it could not be established which facet represents the tuberculum and which the capitulum. Its preserved length is 109 mm.

The collection of Naturalis Biodiversity Center houses an isolated cervical vertebra, which has not been described previously (Fig. 7). The specimen is virtually complete with exception of the anteriormost part of the centrum. Although its morphology generally agrees with those of the specimens discussed above, it differs in exhibiting a much less concave ventral margin of the vertebral centrum. This may indicate that the specimen originates from a different part (possibly the anterior section) of the cervical column than the other specimens, but this cannot be ascertained. Furthermore, although the bone surface appears undamaged, it does not exhibit the laminae present on the vertebral centra of the specimens from the collections of Richard de Haan and Herman Winkelhorst. Such laminae may have originally been absent in this vertebra but, as the fossil appears remarkably smooth, might also have been lost through abrasion, erosion, or weathering.

Finally, it is noteworthy that *Macrocnemus*, a small terrestrial tanystropheid known from Switzerland, Italy, and China, or a closely related form, has been proposed to represent the trackmaker of the ichnogenus *Rhynchosauroides* (Avanzini & Renesto, 2002). *Rhynchosauroides* is an amniote trackway commonly found throughout intertidal laminates in the Winterswijk quarry (Oosterink &



FIGURE 7. | Isolated cervical vertebra from the Naturalis collection (RGM.1332514) in left lateral view. The arrow points anteriorly. Abbreviations: ce, vertebral centrum; dia, diapophysis; epi, epipophysis; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis. Photograph courtesy of Georg Oleschinski (Bonn).



Winkelhorst, 2013). Therefore, if this correlation is correct, *Macrocnemus* would represent a second tanystropheid taxon occurring in the Vossenveld Formation. However this correlation is currently only very tentative, since correlating ichnotaxa to body fossils requires precise comparison and the consideration of various additional factors (Lockley, 1998), and such an in-depth comparison has not yet been provided.

Although still rare and thus far only represented by isolated bones, the presence of tanystropheids in the fauna of the Lower Muschelkalk of Winterswijk is firmly established. Future discoveries in the Winterswijk quarry and elsewhere have the potential to aid in confident clarification of the identity and taxonomic affinity of '*T. antiquus*' and a more complete understanding of its morphology.

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Samenvatting

Tanystropheiden waren Trias-reptielen behorende tot de archosauromorfen gekenmerkt door een lange nek die was opgebouwd uit verlengde wervels en ribben. Dit opvallende kenmerk was het sterkst ontwikkeld in *Tanystropheus*; het meest herkenbare genus binnen deze groep. Een geïsoleerde wervel uit de Winterswijkse Steengroeve werd in 1984 beschreven en herkend als een nekwervel van *Tanystropheus antiquus*. Sindsdien is het genus *Tanystropheus* meerdere malen herzien en wordt de validiteit van de soort *T. antiquus* betwist. Hierdoor is er enige

onduidelijkheid ontstaan ten aanzien van de identiteit van de tanystropheïde resten van de Vossenveld Formatie. Wij presenteren een overzicht van de taxonomische geschiedenis van *Tanystropheus* ten einde de identiteit van de tanystropheïden uit het vroege Midden-Trias, waaronder die uit Winterswijk, op te helderen. Verder worden nog niet eerder gepubliceerde resten van Tanystropheidae uit de Winterswijkse Steengroeve gepresenteerd en beschreven. Ondanks dat het toeschrijven van geïsoleerde resten aan een soort problematisch is zonder dit te kunnen bevestigen uit samenhangende skeletten, worden de gepresenteerde halswervels hieronder voorbehoud toegeschreven aan '*Tanystropheus antiquus*'. De overige elementen, twee halsribben en een ruggenwervel, worden geïdentificeerd als *Tanystropheus* sp.

Institutional abbreviations: **PIMUZ:** Palaeontological Institute and Museum, University of Zurich; **RGM:** Naturalis Biodiversity Center (formerly Rijksmuseum van Geologie en Mineralogie).

REFERENCES

- Ezcurra, M.D., 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* 4: e1778.
- Fraser, N.C. & O. Rieppel, 2006. A New Protorosaur (*Diapsida*) from the Upper Buntsandstein of the Black Forest, Germany. *Journal of Vertebrate Paleontology* 26(4): 866-871.
- Huene, F.R. v., 1907-1908. Die Dinosaurier der europäischen Triasformation. *Geologische und Palaeontologische Abhandlungen Supplement* 1: 1-419.
- Nosotti, S., 2007. *Tanystropheus longobardicus* (Reptilia, Protorosauria): Re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, northern Italy). *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 35: 1-88.
- Peyer, B., 1931. Die Triasfauna der Tessiner Kalkalpen II. *Tanystropheus longobardicus* Bass. sp. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 50: 9-110.
- Pritchard, A.C., A.H. Turner, S.J. Nesbitt, R.B. Irmis & N.D. Smith, 2015. Late Triassic tanystropheids (Reptilia, Archosauromorpha) from Northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. *Journal of Vertebrate Paleontology*: e911186.
- Sennikov, A.G., 2011. New tanystropheids (Reptilia: Archosauromorpha) from the Triassic of Europe. *Paleontological Journal* 45(1): 90-104.
- Skawiński, T., M. Ziegler, Ł. Czepiński, M. Szermański, M. Tałanda, D. Surmik & G. Niedźwiedzki, 2017. A re-evaluation of the historical 'dinosaur' remains from the Middle-Upper Triassic of Poland. *Historical Biology* 29(4): 442-472.
- Wild, R., 1973. Die Triasfauna der Tessiner Kalkalpen XXII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). *Schweizerische Paläontologische Abhandlungen* 95.
- Wild, R. & H.W. Oosterink (1984). *Tanystropheus* (Reptilia: Squamata) aus dem Unteren Muschelkalk von Winterswijk, Holland. *Grondboor & Hamer* 5: 142-148.

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